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Altitudinal Limits of Life in Subtropical Mountains: What Do We Know?[1]

STEPHAN HALLOY[2]

ABSTRACT: Present knowledge of the highest altitudinal limits of organisms and their causes is reviewed. Discussion focuses on subtropical latitudes (20–30°) and altitudes above 4000 m. Methods used in high-altitude studies are limited by logistical and biological factors. Use of a comparative convergence-divergence method is encouraged. Terms such as "extreme" are inappropriate in the description of environments with moderate temperature amplitude, positive water balance, and rich soils but low atmospheric pressure. Characters such as slow productivity, frugal behavior, stress tolerance, crypts, large number of stomata, greater development of lungs and circulatory systems, hygromorphy, heliomorphy, protection, insularity, high diversity, and a decreasing plant/animal ratio are considered typical of organisms in these altitudes (hypsophily). Hypotheses explaining some of the characters are discussed.

THIS PAPER IS designed to synthesize in extremely condensed form some results of studies in the Andes during the last 10 yr, together with indications of problems and contradictory evidence that warrant further investigation. Details of specific points are not presented, but a broad synthesis of the situation is given, and a few examples are selected from an abundant literature.

This study is approached by way of five major questions: (1) Why do organisms not reach higher than they do?; (2) What characters do organisms have near their altitudinal limit, which characters are adaptive, and how do they function?; (3) What are the conditions (i.e., soils, climate, etc.) for life near its altitudinal limits?; (4) What methods will answer these questions and how can the answers be tested?; (5) What really are the maximum altitudes reached by plants and animals?

Answers to the questions posed above are relevant not only to biogeography, evolution, and ecology, but also to the conservation and management of high-mountain resources. At the very limits of life, the balance between life and death is easily tipped by human intervention.

METHODS

There are a number of problems related to methods in high-mountain research.

Comparison of data obtained with nonstandardized methods is a major concern. Standardization is especially important in the physical evaluation of the environment. Different thermometers and the way they are placed, for example, can give quite different results in the same microhabitat (Halloy 1985*a*). Differences of this sort must be taken into account when comparing reports in the literature. The problem is, of course, not unique to high-altitude studies.

There are economical and sociological constraints to high-altitude research. Near the highest levels of plants there is no human population, no productivity potential, and, consequently, little funding or interest in road building, research, etc. At these altitudes there are also human biological limits: above 4000 m work capacity decreases steadily, and research efforts above 5000 m involve much hardship.

The main conceptual framework for analyzing information on altitudinal limits is

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[2] Assistant Professor of Ecology, Universidad Nacional de Tucumán, Argentina.

based on biotypological (Cuatrecasas 1968, Monasterio et al. 1984) and convergence-divergence (Halloy 1983*a*) methods. These are fundamentally comparative methods in which the life forms and morphology of organisms, phenology, demography, and other characters are systematically compared in different places to obtain correlations between character variation and environmental gradients. These methods involve the use of transects at different scales (transects within transects) in local, continental, and intercontinental comparisons (Figure 1).

Multivariate analysis provides for recognition of hierarchically important factors; that is, those that may account for the highest percentage of the variation in the character dimension or state. Successive analysis in different localities eliminates factors one by one in a way reminiscent of experimental laboratory research (i.e., the "natural experiments" of Ricklefs 1973; Halloy 1983*a*).

Additional information may be obtained by using well-known taxa as indicators, studying and manipulating demographic parameters, exchanging organisms between localities, using organisms as sensors (e.g., transplant and germination experiments and using plants as phytometers or in bioassays), and growing plants and animals under standard laboratory conditions to study physiological and behavioral reactions.

Altitudinal Limits

The data necessary to answer the question of the actual altitudinal limits reached by plants and animals are scanty, widely scattered in the literature, and often anecdotal. The available information shows some broad trends in altitudinal-latitudinal and longitudinal patterns (Figure 2).

The pronounced decrease in limits at high latitudes and near the equator seems adequately explained as a "snow limit"; that is, short growing season, low temperatures, prolonged snow-lie, and related phenomena (Cockayne 1958, Walter 1977, Tranquillini 1979, Wardle 1985). The explanations for the remarkable subtropical "bulges" of plant limits remain controversial and are of central interest here.

The High-altitude Environment

Although an extensive literature exists for medium altitudes (2000–4000 m), there are few records for higher altitudes.

An important feature of high mountains is their variability. Nonetheless, a series of environmental factors tends to vary in the same way with increasing altitude on different mountains. The most basic of these trends are reduction in air pressure, reduction in temperature, and increase in direct solar radiation and re-radiation. The latter two, and most other distinguishing features of the high-mountain environment, stem from the rarefied atmosphere. Radiation not only increases (although this may vary with cloud condensation layers), but its spectral composition is also changed in favor of shorter wavelengths. For details of other trends, see Walter (1977), Barry (1979), and Halloy (1985*a*). Trends or gradients that are unexpected or have been found to be contrary to widely held beliefs are discussed below.

TEMPERATURE. Diurnal air and bare ground temperature amplitude diminishes with altitude (Dobremez 1976, Barry 1979, Halloy 1985*a*). Values vary considerably from mountain to mountain, mainly correlated with mountain area, but are consistently lower than in neighboring lowlands in the Alps (Ozenda 1955), subtropical mountains, and equatorial mountains. On Cumbres Calchaquíes (26°40′ S) at 4250 m the yearly average of diurnal amplitude for air at 1.5 m is 11.3°C, but at 470 m at the base of the mountain the yearly average amplitude is 12.5°C. The amplitude between highest and lowest monthly means for the same sites is 9.1°C and 12–15°C, respectively (Halloy 1985*a*). On Chimborazo, near the equator, at 4650–4800 m the extreme air temperatures registered in 4 months were +3.5 and −2°C (Troll 1960). The same effect has been shown for temperatures at ground level (e.g., Halloy 1985*a*), although in this case comparisons are complicated considerably by microsite heterogeneity. The cause is related to the "oceanity" effect of decreasing land area of peaks emerging into high air masses. Leaf temperatures behave differently, possibly increasing in amplitude (Körner and Cochrane

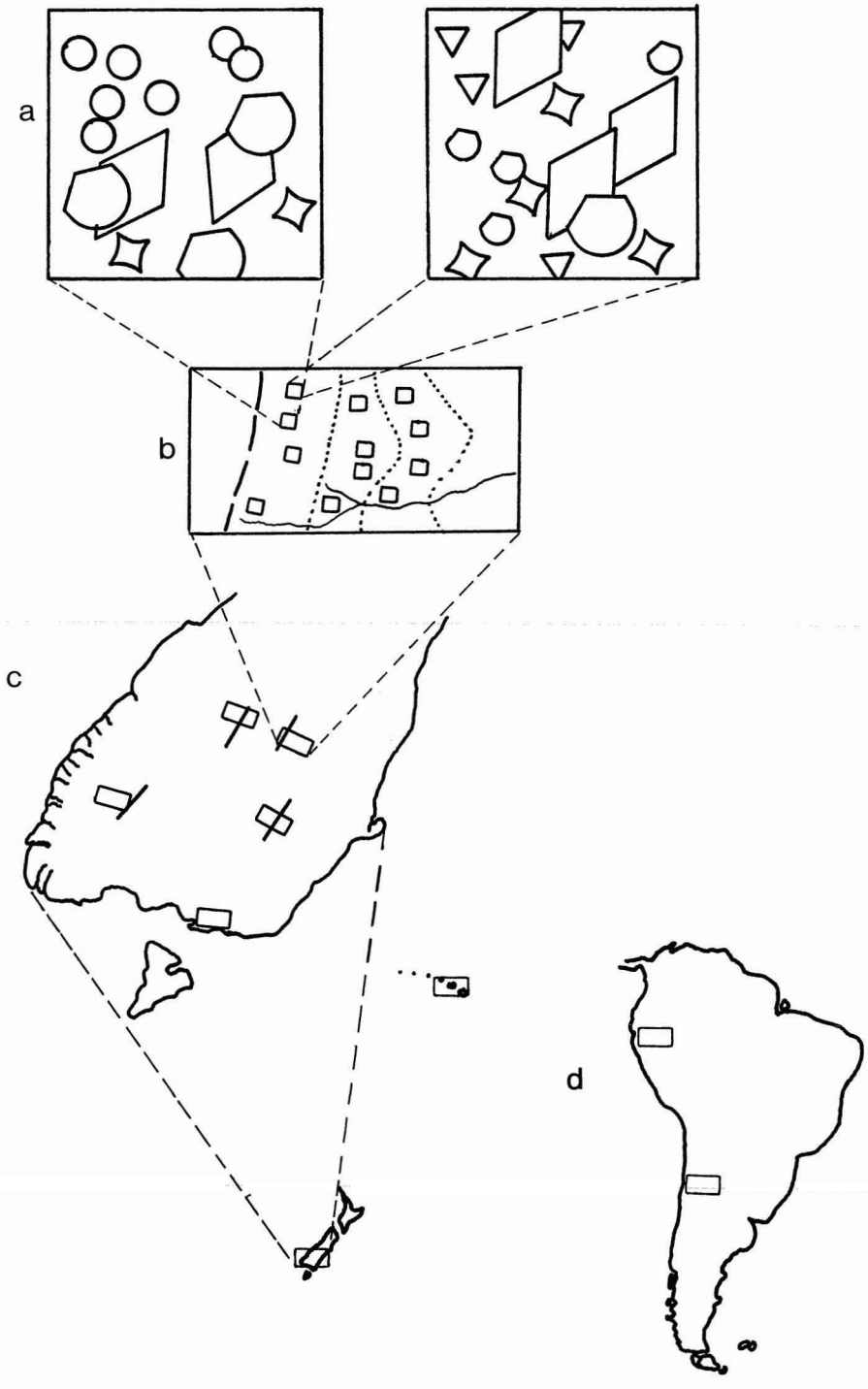

FIGURE 1. Comparison of information from different areas is necessary for a correct interpretation. The scale of this comparison may go from sample to sample (*a*), between communities (*b*, transects), within large regions (*c*, exemplified as southern New Zealand), and global (*d*), Respectively, approximate scales are 1 : 20; 1 : 10,000; 1 : 5,000,000; 1 : 110,000,000. (See also Halloy 1983*a*.)

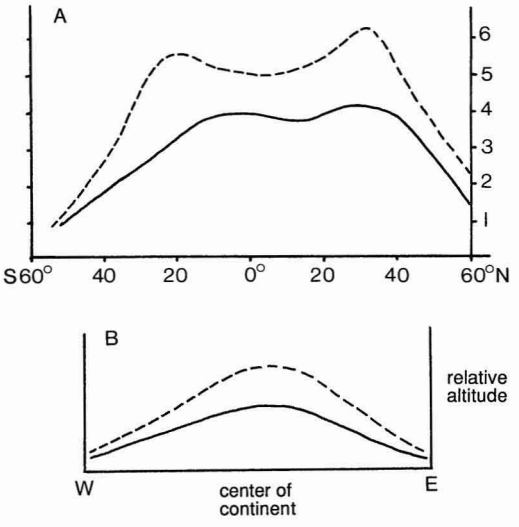

FIGURE 2. Schematic representation of the highest limits of vascular plants (dashed line) and forests (solid line) on a S–N (*A*) and E–W (*B*) line following Daubenmire 1954, Troll 1959, Webster 1961, Coe 1967, Swan 1967, Czajka 1968, and Wardle 1973. Generalization does not permit showing isolated, extreme records, but rather broad tendencies. The asymmetry of the curve towards the north and inland is generally attributed to continentality (see, for example, Herzog 1931, Troll 1947, Meurk 1984). Altitudes in thousands of meters. The E–W curve is of course strongly modified by topography and winds and thus represents only an ideal model.

1983). Some authors maintain that temperature amplitude in general increases with altitude (Coe 1967, Vareschi 1970, Petterssen 1976).

HYDROLOGICAL BALANCE. The hydrological balance tends to become more positive with altitude in arid regions and is generally highly positive in humid regions (Catalano 1927, Halloy 1983*c*, 1984). Maps and aerial photographs of high mountains show that permanent freshwater lakes and rivers are the rule, implying a positive balance between precipitation and evapotranspiration. The presence of uncovered glaciers is also considered an indicator of positive water balance. A more positive water balance is attributed to an increase in precipitation from orographic interception and/or reduced evapotranspiration. In the Cumbres Calchaquíes at 4250 m, about 50% of the precipitation is eliminated by runoff, whereas neighboring valleys in its rainshadow have a deficit at least twice the value of precipitation.

HUMIDITY. Absolute humidity tends to decline due to low temperature and pressure, but relative humidity is often very high, tending to increase with altitude, and evaporation tends to decrease (Braun-Blanquet 1979, Henning and Henning 1981, Iglesias de Cuello 1981, Halloy 1985*a*). This is a relatively straightforward consequence of lower temperatures reducing the vapor pressure deficit. Monthly averages of daily evaporation for the relatively dry subtropical Andes around 4000 m ranged from 3 to 8 mm per day whether calculated or measured in pans (Iglesias de Cuello 1981, Halloy 1985*a*). In contrast, at 470 m, at the base of the same mountains, where there is luxuriant subtropical forest, daily values ranged from 8 to 16 mm per day in summer to minima of 2 mm per day in winter (same method). As a consequence, plants at very high altitudes tend to become less xeromorphic and/or have relatively low water potentials compared with similar plants in equivalent habitats lower down (see below and also Körner and De Moraes 1979). This suggests that vapor pressure deficit will decrease with altitude, although in some particular cases (sun-heated leaves, for example) it may increase (Körner and Cochrane 1983).

OXYGEN AND CARBON DIOXIDE. Partial pressure of carbon dioxide and oxygen diminish with altitude, possibly becoming important selective and even limiting factors (Wager 1934, Dutt and Guha-Thakurta 1938, Halloy 1981, 1983*c*, 1985*a*, Guillette and Jones 1985, and Decker 1947 for timberline). Evidence suggesting that CO_2 partial pressure reaches critically low levels at altitudes above 4500 m is mainly comparative-ecological, showing that under similar thermal conditions, higher sites (where there is less pressure) are considerably less productive (Halloy 1981). Low pressure of oxygen is certainly limiting for animals, and so is CO_2 pressure for plants (in terms of productivity). Yet low O_2 pressure may actually be an advantage to plants in favoring the carboxylase function (C. Körner,

personal communication, 1988) and possibly reducing frost injury (Halloy 1983*c*, 1987).

SOILS. Soils analyzed near vegetation limit often have high cation exchange capacity and mineral fertility (Halloy 1985*a*) although this is inversely related to precipitation, as in lowlands. Nitrogen, for example, is often as abundant as in good agricultural soils (e.g., 0.10–0.44% near vegetation limit in the Cumbres Calchaquíes at 4220–4770 m [Halloy 1985*a*]). If absolute nutrient limitations exist, it may be through interactions with other factors and not per se. Phosphorus is often present in forms unavailable to vascular plants, but has not been measured often enough at very high altitudes to be fully assessed.

OTHER FACTORS. Apart from these general trends, factors that vary locally, for example, geocryogeny (Halloy 1983*d*, 1985*b*), snow cover, and wind (see, for example, Wardle 1985), can also be of great importance.

Characters of Organisms

None of the following characters is unique to high-mountain organisms, and, indeed, some of the characters are similar to those among organisms in lowland cool, moist environments. Nor are all characters present in all organisms found at high altitudes. They are frequently present in organisms on most high mountains, however, and most organisms show a group of these characters as a syndrome of hypsophily (adaptation to low pressures) (Mani 1968, Billings 1974, Halloy 1983*b*,*d*, 1985*a*).

LIFE HISTORY. Low mortality in the youngest phases of life history is tied to a change in reproductive output (increase in size and care of progeny), reduction in litter size, and greater longevity (Halloy 1983*b*, 1985*a*). A classic example is that of high-mountain lizards that produce few young and tend to become viviparous (Fitch 1985, Halloy and Laurent 1987). The same happens in plants like *Polygonum viviparum* and *Poa vivipara* in the Alps. These characteristics imply little ability to replace the dead and have obvious consequences for conservation.

BEHAVIOR. Slow growth and low productivity may relate to thriftiness and altruism, as in the frugal behavior of herbivores like the coleopteran *Pseudomeloe* (Figure 3), the rodent Chinchillon (*Lagydium*) (Halloy 1985*a*), and the camelids guanacos and vicuñas (Cajal 1978, Gonzalez et al. 1986). Behavior of this type is a basically nondestructive way of utilizing resources. For example, when dry leaves rather than green are used, or few leaves are picked at intervals of rather long distances, plant survival is ensured. The most important limiting factor to productivity seems to be low carbon dioxide pressure, although low temperatures and shorter growing seasons also contribute (see above).

STRATEGIES AND LIFE FORMS. Stress-tolerant and colonizing strategies predominate, as most mountains have had fluctuating environmental conditions over the last few thousand years. Competition for light is reduced and leads to life forms of rosettes and cushions (Figure 4). When competition increases, rosettes may tend toward caulirosettes (or stem rosettes) and plurirosette shrubs (Cuatrecasas 1968, Halloy 1985*a*).

ADAPTATIONS TO LOW PRESSURE. Adaptations that promote gas exchange are well known in mammals and birds (Dorst 1963,

FIGURE 3. Female apterous *Pseudomeloe* on *Pycnophyllum convexum* cushion. This beetle spends a lot of energy walking over palatable plants before stopping to eat a morsel and be off again. As a result of this thrifty usage, resources are not locally depleted. Cumbres Calchaquíes, Tucumán, Argentina, 4250 m, 22 December 1978, 17:00 hours, from 24 cm (from Halloy 1985*a*).

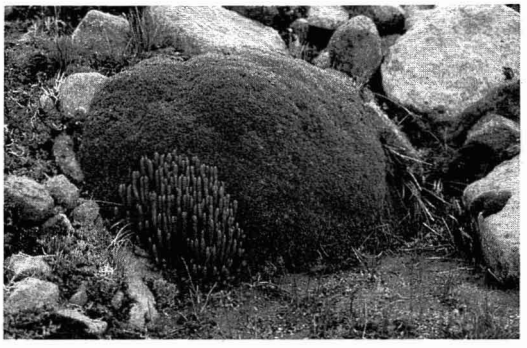

FIGURE 4. Large cushion of *Azorella corymbosa* growing with *Lycopodium* aff. *crassum* near plant limit on a moraine. West side of Antisana Volcano, Ecuador, 4650 m, 3 February 1980, 9:50 hours, from 1.5 m.

FIGURE 5. Revolute hairy leaves in many high-mountain plants form protected "chambers" called crypts, even in superhumid climates as in this case. *Senecio* sp. on moraine, SW side of Chimborazo Volcano at the plant limit, Ecuador, 5055 m, 4 April 1980, 10:40 hours, from 22 cm (from Halloy 1985*a*).

1972, Hock 1970, Heath and Williams 1979), including a greater development of lungs and the circulatory system, and increment in erythrocytes and hemoglobin. Crypts (Figure 5) are also a common adaptation in very high mountain plants, and Halloy (1985*a*) has hypothesized that they favor gas exchange by acting as thermal pumps, thermal filters (when hairs are present), and/or in recycling carbon dioxide. An estimated 30–40% of the flora above 4000 m in the subtropical and equatorial Andes have well-developed crypts. Percentages are even higher (nearly 80%) when excluding ground-hugging species. On the other hand, egg shells reduce their porosity with altitude, as a result of losing more water because of greater diffusivity at low pressure (Rahn and Paganelli 1982).

HYGROMORPHIC CHARACTERS. Many characters of plants in high mountains are hygromorphic; the size and shape of leaves (including finely dissected ones), texture, raised stomata, nutant flowers, relatively high (about −7 to −15 atm in most plants) negative water potentials and/or low osmotic pressure (Hauman 1918, Heilborn 1925, Fischer 1952, Baruch 1979, Halloy 1983*b*, Gonzalez 1985), and prominent leaf sheaths. Other characters can also be found in plants in cool, moist lowland areas. Values of water potential below −20 bar are rare in high-mountain plants, even in the locally driest conditions. Most have values closer to −10 bar. In fact Körner and De Moraes (1979) found water potentials in alpine plants (−4.9 to 6.9 bar) among the highest (less negative) observed. None of these values is even close to values in lowland desert plants, which are up to an order of magnitude greater. In addition, taxa indicative of humid conditions are clearly dominant or present in most high mountains even to such extremes as the filmy fern *Hymenophyllum* at plant limit in Ecuador. Anatomy of roots is often related to waterlogging (Halloy 1983*b*). Even human beings consume less water at higher elevations (for equivalent efforts) (Heath and Williams 1979, Halloy 1985*a*).

ADAPTATIONS TO RADIATION. Adaptations to high light intensities, especially as related to reflection from snow, include behavioral avoidance (as in many mammals and lizards) or hypertrophy of the pecten in birds' eyes. Hairiness and carotenoid pigmentation in plants may in some cases be related to this feature. Radiation is also used directly in heating as in heliothermic lizards and flowers with related adaptations. Many plant characters are clearly heliomorphic; for example, such characters as numerous stomata and thick palisade tissue (Espinosa 1932, Fischer 1952, Halloy 1983*b*, Gonzalez and Ponessa 1985, Körner et al. 1986). High-altitude species are

also more tolerant of ultraviolet radiation than low arctic plants (Caldwell et al. 1982).

PROTECTION. Protective characters such as sclerification, mimicry, apex burial, and hairs may best be related to time (duration of exposure) and longevity (Hinton 1977). Coriaceous leaves may indicate long-lived leaves rather than xeromorphy. In turn, longevity relates to high cost of replacement and low productivity.

INSULAR CHARACTERISTICS. Insular characteristics such as low dispersal capability, low competitive capacity relative to lowland species, and adaptive radiation are also typical of high mountains that are inevitably isolated one from the other (Carlquist 1974, Halloy 1985*a*). Wind dispersal is reduced in plants by a reduction of the flying apparatus (e.g., pappus in composites) together with a proportionately larger seed as compared with that of related species from lower altitudes. The most common type of seed is small (about 1 mm), more or less rounded and smooth, and is included in a dry fruit with no visible dispersal mechanism, which thus excludes animal dispersal. Seeds of this type are found in a large range of different families: in the Cumbres Calchaquíes, at 4250 m, Gramineae, Cyperaceae, legumes, crucifers, Malvaceae, Caryophyllaceae, Juncaceae, Oenotheraceae, and Gentianaceae all have this type of seed. Antidispersal mechanisms are also evident and include reduced pedicels; fruits sticking together in large, heavy groups; and geniculate pappus hairs, hooking onto vegetation (but not to animals). In flying animals (Diptera, Coleoptera, Lepidoptera, and even some birds) wings are often reduced to the point of flightlessness.

PRODUCTIVITY. Toward the highest limits of plants, the local ratio of plant/animal production slowly decreases to less than one, as the animals are "subsidized" by organic matter from outside the system (wind-borne litter). Any plant becoming established at these high altitudes is faced with a host of preestablished potential predators (Swan 1963, Halloy 1981, Edwards 1988), which restricts plant establishment.

There apparently is a parallel trend toward an increase in root/shoot ratio in plants (Monasterio 1979, Halloy 1983*b*), although this varies considerably and needs further research (Smith and Klinger 1985, Körner and Renhardt 1987). There is also a tendency to accumulate large carbohydrate and/or lipid reserves in leaves and subterranean organs (Billings 1974, Bliss and Mark 1974).

Specific leaf area (leaf area/dry leaf weight) for given taxa apparently consistently declines with altitude. A decrease of 25–53% from sea level to 2530 m was found in New Zealand (Körner et al. 1986). On a community scale, total leaf area may often be very large (Vareschi 1953), as expected if gas exchange is a limiting process.

FREEZING TOLERANCE. Both plants and animals seem to be more tolerant of freezing at lower pressures. This is possibly related to lower O_2 pressure inhibiting oxidation processes in the cells after membrane rupture, thus allowing for healing. Both *Bufo spinulosus* (Bufonidae) (Figure 6) and *Liolaemus huacahuasicus* (Iguanidae) revive normally after freezing at $-10°C$ at 4250 m, but they die after freezing at -3 or $-5°C$ at 450 m (Halloy and Laurent 1987). Lettuce in the germination and seedling stage planted at 5445 m tolerated temperatures below $-20°C$ (Halloy 1983*d*) without injury whereas in the lowlands lettuce in the same stages is injured by light frosts ($-1°C$, Halloy, in prep.).

DIVERSITY. Diversity values are remarkably high near the vegetation limit (Table 1). The number of plant species above timberline in New Zealand (Cockayne 1958), the Himalayas (Dobremez 1976), and Tucumán (Halloy 1985*a*) is similar or greater than that below timberline. "Alpine" floras are also generally more diverse than equivalent (as to mean temperature during growing season) arctic floras (Billings 1973). The diversity of alpine floras contradicts generally held views of alpine environments as impoverished due to harsh or extreme conditions. More surprisingly, it also suggests rather abrupt higher limits for a greater number of species instead of a progressive reduction in species richness. This phenomenon has also been observed for ani-

FIGURE 6. The toad *Bufo spinulosus* does not seem to feel the high-altitude environment as extreme. It can freeze in the morning (as here) then call and mate in the evening. Cumbres Calchaquíes, Tucumán, Argentina, 3750 m, 11 August 1977 (from Halloy 1985*a*).

mals: greater or similar species richness of birds (R. Vides, personal communication, 1984) and beetles (M. Molinillo, personal communication, 1984) at 4250 m than in subtropical forests (500–1500 m) at the same latitude (Tucumán, Argentina) with similar sampling techniques.

TWO PARADOXES. There remain two paradoxes of geographical distribution that emphasize the difference between high latitudes and altitudes (see also Mani 1968, Billings 1974): (1) taxa that reach relatively high altitudes within their vegetation type near the equator tend to be well below the corresponding limit at high or middle latitudes (e.g., *Lupinus*, *Geranium*, *Lesquerella*, Ericaceae in

TABLE 1

SPECIES RICHNESS AT HIGH ALTITUDES: TOTAL PLANT SPECIES PER AREA

LOCALE	NUMBER OF SAMPLES	NUMBER OF SPECIES (VASCULAR PLANTS)	ALTITUDE (m)	VEGETATION LINE
Antisana, Ecuador	1	41 per 100 m^2	4,600	Last plants at that locality at 4,700 m; end of continuous vegetation at 4,610 m
Huaca Huasi, Argentina	23	maximum = 27 per m^2 or total > 200 vascular plants in 150 km^2	4,250 4,000 to 4,650	End of continuous vegetation 4,400 m
Niwot Ridge, Colorado	1	19 per m^2	3,750	End of continuous vegetation 3,800 m

America; *Quintinia* and *Dacrycarpus* in Australasia); (2) taxa that reach the highest latitudes tend to live well below the corresponding vegetational limits near the equator (e.g., *Colobanthus*, *Dryas*, *Nothofagus*, *Saxifraga*).

Hypotheses to Explain Altitudinal Limits

Several hypotheses that account for limiting factors are listed below. Where relevant, evidence either supporting or discounting them is cited. A more detailed discussion can be found in Halloy (1985*a*).

SOIL MOVEMENTS. Cryogenic soil movements (Hedberg 1964, Coe 1967) are suggested as explaining some altitudinal limits. At low altitudes with comparable soil movement, there is much more plant cover than at high altitudes whether the movements are cold-induced (high latitude) or otherwise (low latitude). At most, soil movement can only be a conditional and local factor (Halloy 1983*d*, 1985*b*).

SOIL TEMPERATURES. Soil temperatures that are too cold (Walter and Medina 1969, Lauer 1981, and others) is another hypothesis used to explain altitudinal limits. In Ecuador, soil temperatures at 30 cm depth may be as high as +5°C beyond the vegetation limit (4700 m, Antisana) and well above the postulated 0°C limit for that depth. Conversely, plants actually grow on debris on glaciers at lower elevations (Price 1981, Rabassa et al. 1981, Halloy 1983*d*) or in contact with permafrost (Ito 1977). It seems clear that low soil temperature is of relatively low overall importance in explaining the total lack of plants at high altitudes.

AIR TEMPERATURES. Extreme minimum temperatures cannot be the main limiting factor at the highest altitudes because known temperatures are relatively high at those altitudes (minimum −10 to −20°C at plant limit are rarely surpassed) compared to known physiological minima and to arctic values where vegetation is abundant (Larcher 1977, Halloy 1983*d*).

It has been shown that diurnal thermal amplitude (Dobremez 1976) is actually inversely related to altitude in general, so this can surely not be of importance. The number of frost days (Troll 1959, Lauer 1981), however, may be an important limit for some species intolerant of frost.

PHYSIOLOGICAL DROUGHT. One of the most widely held and supported ideas is that water stress is widespread at high altitudes and that it can explain both the limit (Webster 1961, Lauer 1981) and the life forms and adaptations of plants (Hedberg 1964, Ruthsatz 1978, Ancibor 1980). Even when not explicitly stated, this idea is often implicit in the use of such terms as xeromorphic or deserts. The latter term can have various meanings, but it is usually related to aridity and is thus misleading if applied to high mountains (Monasterio 1979). In short, this hypothesis maintains that cold and frost limit water transport and conduction, but warm leaves may continue evaporating, creating a water deficit (Larcher 1977, Tranquillini 1979).

It seems that a certain degree of water stress may select the types of plants present, as in any terrestrial environment, but it may not be important in determining either the highest limit of plants or their life forms. There is also an abundant literature on the subject, although rarely very explicit. There is no doubt that water stress occurs at high altitudes. The question is, does it become so intense that no species of plant can tolerate it? The following evidence may cast doubt on the hypothesis that water stress limits altitudinal distribution: (a) Climatic water balance, humidity, and evaporation data (see above); (b) Characters of plants and plant indicators that suggest low water stress; (c) High-altitude plants are not resistant to drought, and usually die promptly in the laboratory if not constantly watered; (d) Experimental sowings of sunflower, lettuce, and oat seed resulted in good germination and establishment far above timberline and up to plant limits in the Andes (4250 to 5445 m) and New Zealand (2 to 2320 m) without irrigation (Halloy 1983*c*,*d*; in preparation). Subsequent death was rarely related to drought; (e) Frozen or very cold soils may limit water uptake but whether the

resulting water stress when insolation is high can exclude plants is open to query, since plants can be found growing on glaciers in rock rubble. Additionally, "tree roots at Arctic timberline readily conduct water while embedded in frozen soil" (Polunin 1933 *in* Daubenmire 1954); (f) "Soil floating plants" without roots actually occur near vegetation limits and obviously do not even need soil moisture to remain active (Halloy 1983*d*); (g) Experimental irrigation of natural vegetation does not result in differences, except in localized mesotopographic well-drained soils.

The evidence clearly indicates that physiological drought does not explain the altitudinal limit of plants, but water use efficiency does decline with altitude because of low CO_2 pressure (Halloy 1985*a*).

PARTIAL PRESSURE OF CO_2 AND OXYGEN. Although sometimes mentioned as a factor (Billings 1974), low partial pressure of carbon dioxide and oxygen is rarely considered important in determining altitudinal limits. CO_2 partial pressure particularly has been suggested by Wager (1934) and others as a factor. And, indeed, it is possible that CO_2 is actually the ultimate limiting factor for plants at the highest altitudes. It has always been a mystery why plants reach higher altitudes in the Himalayas (6350 m) rather than the Andes (about 5800 m). But if pressure at these sites is measured, it is similar, approaching 480 mb (Halloy 1983*d*, Moore 1968) because of different regional pressure gradients.

EVOLUTIONARY TIME AND BIOGEOGRAPHY. Considerable climate fluctuation has occurred in recent time and can be expected to have eliminated numerous organisms at very high altitudes. Glaciations may be the most serious of these climatic changes (Lauer 1981, Halloy 1985*a*). Other local catastrophes such as landslides, earthquakes, and vulcanism may also be important (Halloy 1983*c*). Thus, organisms adapted to the lowest pressures may have been decimated, and a prolonged period must be allowed for reinvasion of the highest sites (see below). This is especially clear in cases where source areas are too distant for colonization; for example, in Hawaii where the case may be invasion rather than re-invasion.

The paradox of high diversity just below the limits may also relate to catastrophes with abrupt limits such as glaciation.

In contrast to arctic areas that experienced glaciations, the biogeographical scale of colonization at high altitudes seems to be considerably prolonged. There are several reasons for this, among them the greater relative intensity of recent catastrophes such as the "little ice age," slow growth and hence reproduction, lack of adapted species because of the restricted areas available and because of extinctions, low dispersal capability, and consumer balance in favor of predation or consumption at high altitudes.

DISCUSSION AND CONCLUSIONS

It is clear that knowledge of life and environments in the high subtropical mountains is meager. It is also clear that the combination of poor knowledge and inadequate analytical methods and comparisons has led to generalizations about high-mountain environments and biotas that are untenable. Alpine environments are often considered "extreme," with factors such as water stress, high temperature amplitude, low temperatures, strong wind, and high radiation thought of as limiting to life (Wall 1925, Daubenmire 1954, Hedberg 1964, Monasterio 1979, Ancibor 1980). This oft-cited "extremeness" of high-mountain environments needs revision, and the term should be used only with respect to the magnitude of a particular factor (Halloy 1985*a*).

Several hypotheses proposed to explain altitudinal limits need revision. Water stress in high mountains, for example, seems incapable of accounting for the lack of plants above the vegetation limit if the facts of the hydrology of high mountains and the physiology of plants are considered. Indeed, the hypothesis of water stress has led to underestimating high mountains as water producers and to overestimating the capacity of man to increase production by irrigation (e.g., Peruvian Agrarian Reform plans). Water stress, as in most terrestrial environments, does exist and

is measurable, but it is often less than in lowlands with abundant biomass at the same latitudes.

The data suggest that high-mountain communities are in a sort of evolutionarily extended primary succession. The cause of destruction that left areas bare is usually past climatic fluctuation, particularly glaciation, but also drought, floods, as well as other catastrophes such as vulcanism and landslides. In contrast to arctic areas that suffered glaciations, colonization in high-altitude communities is prolonged because of the characteristics of the physical environment and because of the adaptations of the organisms that live in that environment. Although this hypothesis may explain in general most of the highest limits of plants, it must be emphasized that mountains are extremely diverse, and other explanations are possible (Gomez Molina and Little 1981).

It is also of interest to realize that any parameter of the actual environment will have some causal relation with past environments (cool environments are actually closer to past glaciated areas than warm ones). Thus, if we find a common value of temperature near plant limits in the Rocky Mountains, it may be related to their present physiological limits, but it may also be explained as an indicator of the severity of past glaciations, as in the model in Figure 7. The relation between past conditions and present limits is established through slowness of colonization.

Future tests of hypotheses should include a greater knowledge of the environment and biotas; more comparisons on a wide scale, using convergence and divergence as indicators of evolutionary trends; field and laboratory experiments controlling one or more of the factors (irrigation, fertilization, greenhouses, etc.); the use of known plants as sensors or bioassays of the environment; detailed observations and measurements of exceptional local conditions such as warm springs, giving rise to "natural experiments" (see, for example, Hedberg 1959, Halloy 1986); and caution in the use of extrapolation. Much of our knowledge on altitudinal gradients of factors and characters is from transects up to 3000 m. Very few pass 4000 m. Linear extrapolation from these is not always justified.

High-mountain areas offer clear scientific challenges. They must be better known if they are to be managed correctly (Billings 1973, 1978).

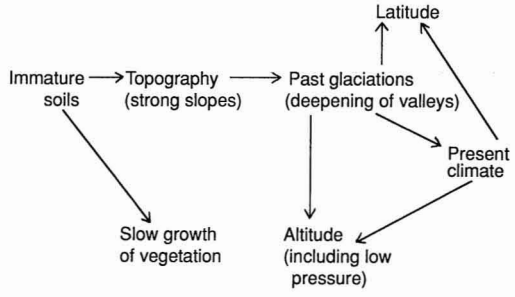

FIGURE 7. Interrelation between past and present factors related to vegetation altitudinal limit.

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